Ecological implications of pedogenesis and geochemistry of ultramafic soils in Kinabalu Park (Malaysia)

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Abstract

In Sabah, Malaysia, ultramafic rock outcrops are widespread (totalling 3500 km^2, one of the main outcrops in the tropical zone), and predominantly of the peridotite type. However, strongly serpentinised peridotite is also locally common, particularly along fault lines in the Mt. Kinabalu area. This study aimed to determine the extent of chemical variation in ultramafic soils in relation to the degree of serpentinisation and the weathering intensity, and consequent potential ecological implications linked to resulting soil chemical fertility. It was hypothesized that young soils and soils derived from bedrock with a significant degree of serpentinisation strongly differ from typical Geric Ferralsols and result in soil chemistries with more adverse properties to plant life (e.g. low availability of the essential nutrients N, P, K and Ca and high concentrations of potentially phytotoxic Mg and Ni). Ultramafic soil diversity linked to the age of the soil or the degree of serpentinisation would thus be a main factor of plant diversity and distribution. The diverse topography of Kinabalu Park (ultramafic soils present between 400 and 2950 m asl) has given rise to high pedodiversity with the broad overall ultramafic soil types being: (i) deep laterite soils (Geric Ferralsols); (ii) moderately deep montane soils (Dystric Cambisols) with mor humus; (iii) shallow skeletal soils at high altitude (Eutric Cambisols Hypermagnesic); and (iv) bare serpentinite soils (Hypereutric Leptosols Hypermagnesic) at low altitude (200–700 m asl). Leptosols on serpentinite and Eutric Cambisols have the most extreme chemical properties in the whole Kinabalu Park area both with very high Mg:Ca molar quotients, with either high available Ni (Cambisols) or high pH (Leptosols). These soils host specific and adapted vegetation (high level of endemism) that tolerates geochemical peculiarities, including Ni hyperaccumulators. Geric Ferralsols present far less chemical constraints than Hypermagnesian Cambisols soils to the vegetation and host a tall and very diverse rainforest, not so different than that on non-ultramafic soils. It therefore appears that altitude, soil age and degree of bedrock serpentinisation are the main determining factors of soil properties: the qualifier "ultramafic" alone is not sufficient to define soil geochemical and ecological conditions in the Kinabalu Park area, probably more than in any other ultramafic region in the world.

Introduction

Properties of ultramafic soils

Ultramafic bedrock is part of the upper mantle (peridotite) obducted in continental margins (Searle and Stevens, 1984). Such outcrops are widespread but relatively rare, covering > 3% of the surface of the earth (Guillot and Hattori, 2013). The largest ultramafic regions in the world can be found in temperate (e.g. Balkans, Turkey, California) and in tropical environments (e.g. New Caledonia, Cuba, Brazil, Malaysia, Indonesia). Southeast Asia has some of the largest tropical outcrops in the world with Borneo and Sulawesi together totalling over 23,000 km^2 (van der Ent et al., 2013; Galey et al., 2017). The rock-type peridotite is made up from magnesium-iron-silicates in the minerals olivine and (ortho)pyroxene (Coleman, 1971). Low-temperature hydration and metamorphism of peridotite leads to serpentinite, usually at the sea floor along tectonic boundaries (such as near mid-ocean ridges) or during continental emplacement (Lewis et al., 2006; Guillot and Hattori, 2013). During serpentinisation, the mineral assemblage is completely altered to metamorphic equivalents, and only chromite usually remains unaltered (Coleman, 1971; Alexander, 2009). Serpentinite rocks contain very high Mg (18–24%) and high Fe (6–9%) but low Ca (1–4%) and Al (1–2%) (Alexander, 2004). The total transformation of peridotite to serpentinite needs 14% water and the rock expands by 33% from dense peridotite (3.2–3.3 g cm3) to less dense serpentinite (2.4–2.6 g cm^3) (Alexander, 2009). This results in fracturing and shearing of the rock, and as such, the weathering properties of serpentinite rocks are dramatically different from peridotite bedrock. All near-surface ultramafic rock is serpentinised to varying degrees, and serpentinite is used to describe rocks containing > 50% serpentine- group minerals (i.e. antigorite, chrysotile, lizardite) in which the original (primary, or not metamorphosed) mineralogy is obscured. Ultramafic rock generally itself only contains 0.16–0.4% nickel (Butt, 2007) however these initial concentrations increase significantly during sur- face weathering in humid tropical climates, resulting over the long term, in nickel laterite soils (Echevarria, 2018). Such nickel-enriched ultramafic soils are a major target for the nickel and cobalt mining industries, particularly in tropical settings such as in Cuba (Roqué-Rosell et al., 2010), Brazil (Colin et al., 1990), Indonesia, the Philippines and New Caledonia (Butt, 2007; Fan and Gerson, 2011).

Properties commonly shared among ultramafic soils include high iron (Fe) and magnesium (Mg) concentrations and low aluminium (Al) concentrations, relatively high concentrations of chromium (Cr), cobalt (Co) and nickel (Ni), high magnesium-to-calcium (Mg:Ca) quotients in the exchange complex and low concentrations of phosphorus (P) and potassium (K) (both total and extractable). In ultramafic laterites (i.e. Ferralsols), some of these features might be less strongly marked be- cause intense weathering has erased the fingerprint of geochemical peculiarities: i.e. a higher aluminium (Al) concentrations and lower magnesium-to-calcium (Mg:Ca) quotients than in ultramafic Cambisols or Luvisols (Echevarria, 2018).

Geology of ultramafic outcrops in Kinabalu Park

Ultramafic outcrops cover 3500 km^2 in Sabah (Proctor et al., 1988; Repin, 1998) and 151 km^2 in Kinabalu Park (Fig. 1a). The ultramafic rocks are part of an ophiolite suite which derived from a collision suture between the Kalimantan micro-continent and the Sulu Arc (Imai and Ozawa, 1991) when oceanic lithosphere of the Sulu Sea was obducted (McManus and Tate, 1986). Mount Kinabalu (4095 m) is a granite intrusion dated 7.2 to 7.9 Ma before present (Cottam et al., 2010) and ultramafic outcrops form a ‘collar-like’ distribution on the mid-elevation around the Kinabalu granite core. In the northern part of Kinabalu Park lies Mount Tambuyukon (2579 m). Of the outcrops in Kinabalu Park, Mount Tambuyukon is the largest (89 km^2), but many small outcrops (< 1 km^2) also exist especially around Mount Kinabalu (Fig. 1b). In the Kinabalu area the most common peridotite is lherzolite, and tremolite-bearing peridotites whereas harzburgite and wehrlite are rare (Jacobson, 1970).

Pedogenesis and mineralogy of ultramafic soils

Ultramafic bedrock contains on average approximately 0.2% Ni, 0.02% Co, 10% Fe and 0.2% Cr (Butt and Cluzel, 2013). A recent article summarises the main factors involved in ultramafic soil pedogenesis (Echevarria, 2018). In tropical settings, weathering of ultramafic bedrock leads first to secondary phyllosilicates (Cambisols), then to amorphous and poorly-crystalline Fe-Cr-Mn oxides, and finally to crystalline Fe-oxides (Schwertmann and Latham, 1986; Becquer et al., 2006; Echevarria, 2018). In well-drained soils, peridotite minerals (olivine and pyroxenes) weather to form secondary (Fe-rich) minerals (goethite, hematite), and Mg and Si move down the soil profile and accumulate at depth (Latham, 1975b; Trescases, 1975; Proctor, 2003) whereas Fe, Cr and Al are less soluble and remain higher up in the profile. Nickel is also highly leached during pedogenesis, in contrast to other metals, e.g. Al (Estrade et al., 2015; Echevarria, 2018). The results are deep red 'laterite' soils consisting of a limonite (Fe-oxide) layer and a saprolite (Mg, Si-rich) layer (Gleeson et al., 2003). Total Cr concentrations are generally very high in the limonite layer. The secondary Fe and Mn oxides are known to be a major sink for Ni because of their high sorption capacity (Becquer et al., 2001), often containing 0.8–1.5 wt% Ni (Fan and Gerson, 2011). The Ni, Mg and Si leached into the saprolite are the main 'ore' mined in the lateritic nickel mining industry, where Ni is embedded in phyllosilicate minerals (Freyssinet et al., 2005) as a substitution for Mg. This layer can contain up to 5 wt% Ni, and in garnierite over 20 wt% Ni (Fan and Gerson, 2011), but the average is 2–3 wt% (Elias, 2001). The nature of secondary phyllosilicates in saprolites varies according to the composition of the peridotite (total Si content) from serpentine minerals to Fe-rich smectites (Raous et al., 2013). Well-drained profiles can be 20 m deep in the Philippines (Fan and Gerson, 2011) and New Caledonia (Latham, 1975b; Dublet et al., 2012) or even deeper, for example in Niquelândia, Brazil (Colin et al., 1990), but are usually < 10 m in Sabah. These regoliths are termed 'nickel laterites' (Butt and Cluzel, 2013), 'sols ferralitiques ferritiques', or 'Geric Ferralsols' (Latham, 1975b; Becquer et al., 2006). Ferralsols can occur on serpentinite which produces a smectite-rich saprolite material such as for pyroxenite (Echevarria, 2018). Due to the high susceptibility of erosion that can affect smectite-rich saprolites, Ferralsols on serpentinite are seldom observed because they are easily truncated (Echevarria, 2018); such laterites, when reported, are usually extremely old and occur in flat landscape positions (Yongue-Fouateu et al., 2006). Ferralsols can also form in the montane zone on steeper slopes, but these soils are much shallower and do not feature an extensive limonitic layer and often have (in the upper montane zone) significant build-up of organic matter (mor-type humus). In the New Caledonian context, these soils are termed 'sols à accumulation humifère' (Latham, 1975a, 1975b) or 'Inceptisols' (tropepts) in the USDA classification (Burnham, 1975; Bruijnzeel et al., 1993). Between the two extremes many varieties exist as a result of local erosion, colluvium and climate (Jaffré, 1992). At high altitude, very shallow skeletal soils (Cambisols) form, which are a direct product of primary weathering of the bedrock, close to the surface. Excess Si recrystallises to form quartz and chalcedony and excess Mg reacts with atmospheric carbon dioxide and precipitates as magnesite (Proctor, 2003). These soils ('Eutric Cambisols Hypermagnesic' or 'sols bruns eutrophes hypermagnésiens' viz. Jaffré and Latham, 1974; Latham, 1975a; Jaffré, 1980; or 'Hypermagnesic Hypereutric Cambisols' viz. Chardot et al., 2007) have extremely high Mg:Ca quotients as well as high available Ni as a result of the disintegration of phyllosilicates and re-sorption onto secondary Fe-oxides or high-charge clays (Bani et al., 2014; Estrade et al., 2015; Echevarria, 2018).

Coleman and Jove (1992) emphasised the importance of distinguishing between the weathering of peridotite, and serpentinite derived from peridotite, the first being mineralogically extremely unstable and the latter relatively stable. Serpentine mineral dissolution under surface conditions is a rather slow process compared to the dissolution of olivines or pyroxenes (Chardot-Jacques et al., 2013). More recently, a study showed how peridotites and serpentinites influence soil composition and metal geochemistry in a different way under temperate conditions (Kierczak et al., 2016). The mineral composition of azonal serpentinite soils (i.e. soils derived from disintegrated serpentinite colluvium, probably Cambisols) therefore contains both primary minerals (chrysotile, antigorite, lizardite) and secondary minerals (smectites, magnetite, chlorite, talc) (Chardot et al., 2007; Bani et al., 2014). Generally, Ferralsols and Dystric Cambisols are oligotrophic with very low base saturation and very low and low CEC, respectively, whereas hypermagnesian Cambisols and serpentinitic Leptosols are eutrophic (sometimes dystrophic) with high base saturation and CEC (Echevarria, 2018). Ferralsols, as per definition, have no weatherable minerals in the ferralic horizon. Cambisols have a Bw (weathering) diagnostic horizon where weatherable minerals are significant in proportion, which includes high activity clays resulting in a high CEC (> 24 cmol kg $^{-1}$). 'Montane inceptisols' are classified as Cambisols in the WRB, but have many similarities with Ferralsols (they have most of the ferralic properties except the depth development).

Trace element speciation and toxicity in ultramafic soils

Although nutrient limitations and cation imbalances have been frequently studied as a cause of the disjunct vegetation on temperate ultramafic soils (Walker et al., 1955; Proctor, 1970; Nagy and Proctor, 1997), relatively high total concentrations of the trace elements Ni, Cr and Co in ultramafic soils have also been linked to potential phytotoxic effects (Brooks, 1987; Proctor, 2003). However, in humid tropical conditions, the most important factor in controlling ultramafic vegetation development seems to be soil depth (Proctor et al., 1999). The potential effects of Ni, Cr, Co and Mn toxicities on native rainforest vegetation as a whole are largely unknown, however, despite clear evidence of toxicity of these elements to plants in experimental work (Anderson et al., 1973; Taylor et al., 1991; L'Huillier et al., 1996). Nickel, in particular, has been attributed as one of the main causes for the stunting of some types of ultramafic vegetation (Brooks, 1987; Brady et al., 2005), but it is probable that other geochemical factors such as low nutrient (i.e. K and P) concentrations – or combinations of Ni stress and low K and P – also play a role in these phenomena (Proctor, 2003). The phytotoxicity of Ni depends mainly on soil-specific chemistry, in particular the mineralogy of Ni-bearing phases (high-exchange clays and poorly-ordered hydrous Fe and Mn oxides contain available forms) and soil acidity (pH decreases Ni adsorption to release phytotoxic Ni ions) (Hunter and Vergnano, 1952; Crooke, 1956; Halstead, 1968; Echevarria, 2018). In laterite soils, Ni is predominantly associated with crystallised Fe-oxides (such as goethite) and Mn-oxides (such as birnessite and lithiophorite), whereas in serpentinite soils, Ni is predominantly associated with phyllosilicates and smectite clay minerals when they form (Lee et al., 2003; Massoura et al., 2006; Fan and Gerson, 2011; Dublet et al., 2012; Bani et al., 2014). Despite very high total concentrations, extractable/phytoavailable concentrations of chromium are generally low as soil Cr-bearing minerals (such as chromite, Cr-magnetite) weather extremely slowly (Oze et al., 2004; Garnier et al., 2006). However, Cr-VI pools in such soils can reach high concentrations (approx. 0.1 wt%) and are often highly available (Garnier et al., 2009). Although Co is relatively more soluble in ultramafic soils compared to Cr, it is present at much lower total concentrations than either that metal or Ni, and its fate is specifically associated with that of Mn. Also, very little is known about any (toxic) effects Co might have on plants growing in tropical ultramafic soils.

Ultramafic ecosystems in Kinabalu Park

Kinabalu Park is renowned for its plant diversity with over 5000 recorded plant species (Beaman, 2005; van der Ent et al., 2015a), partly the result of its variety of soils derived from a range of contrasting bedrock types (i.e. high 'geodiversity'). Chemical characterization of ultramafic soils is important for understanding the ecology and plant/ soil interactions of these ecosystems and the specific role played by intrinsic ultramafic rock diversity in the overall species richness and diversity of Kinabalu Park. Although the distinctiveness of ultramafic soils compared to non-ultramafic soils is often emphasised (Brooks, 1987), it is not generally acknowledged that ultramafic soils themselves vary greatly in their chemical characteristics, and important differences between plant community compositions on different ultramafic soils, at the same altitude, have also been observed (Borhidi, 1999). Although the term 'serpentine' is frequently used to describe ultramafic geology, this is incorrect, as serpentine group minerals are only a subset of those associated with ultramafic rocks (Brooks, 1987; Brady et al., 2005). Nickel hyperaccumulator plants in Sabah were found to occur exclusively on young soils (Cambisols) that were found on strongly serpentinised bedrock (van der Ent et al., 2015b; van der Ent et al., 2016a).

This study aimed to determine the extent of chemical variation in ultramafic soils in Kinabalu Park in relation to the level of serpentinisation and weathering intensity, and consequent potential ecological implications linked to soil chemical fertility. Firstly, the objective was to compare ultramafic soil geochemistry to adjacent non-ultramafic soils to verify the existence of a geochemical shift on this substrate. Secondly, it was hypothesized that soils young soils on peridotite with low amounts of serpentine minerals, and all soils derived from serpentinite (i.e. containing > 50% serpentine minerals after Jacobson, 1970) bedrocks (i.e. serpentinite vs. peridotite) result in soil geochemistry with more adverse properties to plant life (e.g. low availability of essential nutrients and high concentrations of potentially phytotoxic Mg, Cr and Ni). In total, 87 non-permanent vegetation plots were established covering all major 12 'ultramafic edaphic islands' known in Kinabalu Park. In each 'island', at least four plots were laid out, with plot sizes determined by altitude. The altitude ranged from 474 to 2950 m above sea level (asl).

Materials and methods

Site survey and sample collection

Fig. 1a shows a shaded relief map of Sabah with the major ultra- mafic occurrences, whereas Fig. 1b shows the overall geology and main ultramafic outcrops in the study area. Soil profiles were observed and soil and bedrock samples were collected from 13 different ultramafic sites in Kinabalu Park, within an area of approximately 700 km^2 as part of an ecological study (for details refer to van der Ent et al., 2016b). The objective in the sampling was to account for the geological variability within ultramafic rocks (from non-serpentinised peridotite, including dunite, to serpentinite) as well as for edaphic and vegetation variability. Therefore, bedrock samples were carefully observed during the field survey to determine if they were from the serpentinite type or the non- or poorly-serpentinised peridotite type. For some of these samples, further X-ray diffraction mineralogy was used to confirm the observations and the local available descriptions of ultramafic rock outcrops (Jacobson, 1970; Imai and Ozawa, 1991; Tashakor et al., 2017). In particular, the degree of serpentinisation of peridotites is well documented in the Mount Kinabalu area (Jacobson, 1970; Tashakor et al., 2017). However, the Mt. Tambuyukon area (including the Serinsim lateritic plateau) is less documented (van der Ent et al., 2016a). Table 1 reports relevant site attributes (altitude, slope, bedrock type, soil type, soil depth, vegetation) and the number of samples collected from each site. At each site, at least three soil samples (1–2 kg) and one bedrock sample (2–3 kg) were collected. Each soil sample was collected in the A1 horizon, and care was taken not to include fresh organic constituents in surface layers. The bedrock samples were collected from a soil pit at each site. The sites ranged in elevation from 474 to 2950 m and included a total of 95 discrete sample localities (dispersed within each ultramafic site). In addition to the shallow soil samples, five soil profiles were also excavated and samples were collected from all horizons down to the bedrock. Non-ultramafic soil and bedrock samples were collected from Kinabalu Park, near Park Headquarters (1550 m), around Layang- Layang (2700 m) and from nearby Mount Trus Madi (1600–2450 m) to serve as a comparison dataset to contrast the ultramafic soils and bedrock. The underlying bedrock from the non-ultramafic soils was sandstone, shale and granite. Soil profiles were described at a 36-m deep profile near Hampuan on strongly serpentinised peridotite (i), a 22 m deep profile at Sunsui with a full limonite to saprolite layering (ii), a 0.9 m deep profile in lateritic (Ferralsol) regolith near Serinsim (iii), and two profiles in serpentinitic Leptosols, 0.75 m and 0.9 m deep, respectively, near Wuluh River (iv and v). All soil samples were packed, brought to the local field station, air-dried at room temperature to constant weight (3–4 weeks), sieved to < 2 mm, shipped to Australia, and gamma irradiated at Steritech Pty. Ltd. in Brisbane following Australian Quarantine Regulations. The rock samples were treated identically to the soils, but were dried in an oven at 70 °C for 48 h and ball-milled and sieved to < 100 μm fraction.

Laboratory analyses: soil chemistry

The analysis of the soil samples took place at the laboratory of the Centre for Mined Land Rehabilitation (CMLR) at The University of Queensland in Australia. The soil samples (300 mg) were digested using freshly prepared Aqua Regia (9 mL 70% nitric acid and 3 mL 37% hydrochloric acid per sample) in a microwave for a 1.5-hour programme and diluted to 45 mL with ultrapure (TDI) water before analysis. This method yields 'pseudo-total' elemental concentrations in soil matrices (viz. Rayment and Higginson, 1992). Soil pH and electrical conductivity (EC) were obtained in a 1:2.5 soil:water mixture. Plant-available phosphorus ('ML-3') was extracted with Mehlich-3 solution consisting of (0.2 M CH_3COOH + 0.25 M NH_4NO_3 + 0.015 M NH_4F + 0.013 M HNO_3 + 0.001 M EDTA at pH 2.50 ± 0.05) according to Mehlich (1984). Labile ('lab.') Ni, Co, Cr and Mn were extracted in 0.1 M Sr $(NO_3)_2$ at a soil:solution ratio of 1:4 (10 g:40 mL) and 2 hour shaking time (adapted from Kukier and Chaney, 2001). As a means of esti- mating potentially plant-available trace elements, DTPA-Ni, Co, Cr and Mn were extracted with diethylene triamine pentaacetic acid (DTPA) according to Becquer et al. (1995), which was adapted from the original method by Lindsay and Norvell (1978), by the following modifications: excluding TEA, adjusted at pH 5.3, here an extraction time of 2 h was used (instead of 1 h) and a soil:solution ratio of 1:4 as Kukier and Chaney (2001) have demonstrated that the DTPA can be oversaturated with Ni in Ni-rich soils. A second method (loosely based on Feng et al., 2005) for extracting phytoavailable ('CA') Ni, Co, Cr and Mn was also employed, and used carboxylic acids (acetic, malic and citrate acid in molar ratio of 1:2:2 at 0.01 M) at a soil:solution ratio of 1:4 (10 g:40 mL) and 2 hour shaking time. Exchangeable cations ('exch.') were extracted with silver-thiourea (Dohrmann, 2006) over 16 h.

Ni, Co and Cr partitioning was evaluated with a 5-step selective sequential extraction scheme to provide operationally defined solid- phase trace element (Ni, Cr, Co, Mn) fractionation. This scheme is based on Quantin et al. (2002), which was in turn modified mainly from Leleyter and Probst (1999). Adaptations were made here by combining step 1 and step 2, and by using HNO3/HF high-pressure microwave digests for the residual fraction (step 5) instead of an alkaline fusion as in Quantin et al. (2002). The step for the 'organic bound phase' was also omitted because the tested soils are extremely low in organic matter. As such the fractions were: water soluble and exchangeable (i), bound to Mn oxides (ii), bound to amorphous Fe oxides (iii), bound to crystalline Fe oxides (iv), and residual (v). After each extraction step, the tubes were centrifuged for 10 min at 4000 rpm and the supernatants were then filtered through 0.45 μm membranes.

The residues were washed with 20 mL of TDI water, centrifuged again for 10 min at 4000 rpm, the water decanted, and the residue dried at 40 °C prior to the next extraction step. All soil extractions were undertaken in 50 mL polypropylene (PP) centrifuge tubes. Soil samples were weighed using a 4-decimal balance. Samples were agitated for method-specific times using an end-over-end shaker at 400 rpm, centrifuged (10 min at 4000 rpm) and the supernatant collected in 10 mL PP tubes. All soil samples were analysed with ICP-AES (Varian

Vista Pro II) for Ni, Co, Cu, Zn, Mn, Fe, Mg, Ca, Na, K, S and P. Each method included three sample blanks, two NIST standards, two ASPAC reference soils, three random sample duplicates and three multi-element standards as part of the quality control. The ICP-AES instrument was calibrated using a 6-point multi-element standard (Ni, Cu, Fe, Mg, Ca, K) prepared in each extraction solution.

Total elemental concentrations in rock samples (100 mg) were obtained by digestion with a mix of 4 mL 70% nitric acid, 3 mL 37% hydrochloric acid and 2 mL 32% hydrofluoric acid per sample in a microwave for a 2-hour programme and diluted to 45 mL before analysis. The aliquots were also analysed with ICP-AES as detailed above.

Laboratory analyses: soil and rock mineralogy

Bedrock and soil samples were analysed for mineral constituents at the University of Rhode Island, Department of Geosciences (Kingston, RI). Samples were individually powdered using percussion mortar and manual mortar and pestle, and passed through a 150-micron sieve. X- ray diffraction (XRD) profiles were collected with an Olympus (formerly InXitu) Terra Mobile XRD System, a field portable unit with extremely robust performance (Blake et al., 2012). The Terra is outfitted with a micro-focus X-ray tube (nominal operating voltage of 28 keV, filament current of 1.5 A, cathode output of 100 μA) with a Co anode, which yields continuum and characteristic X-radiation from a 50 μm diameter spot on the Co anode (Blake et al., 2012). 250 exposures generate a well-defined diffractogram for comparison with reference data files. Minerals were thus detected in the complex natural mixtures by comparing sample diffractograms with known reference diffractograms for individual minerals. Similarly, mineral phases were detected in soil samples from the profiles with a Bruker D8 Advance X-Ray diffractometer (at The University of Queensland, Australia) equipped with a copper target, diffracted-beam monochromator, and scintillation counter detector. Conditions for running the samples were: 40 kV, 30 mA, 3–80° 2 θ, 0.05° step size or increment, with 10 s per step.

Statistical analysis

The soil and rock chemistry data was analysed using the software package STATISTICA Version 9.0 (StatSoft), Excel for Mac version 2011 (Microsoft) and PRIMER Version 6 (PRIMER-E). The XRD data was analysed with the XPowder software program (version 1.0), and with DIFFRACplus Evaluation Search/Match Version 8.0 and the International Centre for Diffraction Data's PDF-4/Minerals database. The map was prepared in ArcGIS version 10 using geological database files prepared by Robert Hall (Royal Holloway University, London).

Non-metric multidimensional scaling (NMDS) is routinely used ordination technique for soil and plant data. NMDS of pseudo-total soil elements (A) and exchangeable and extractable elements (B) from all collection sites, contrasted with non-ultramafic comparison soils was carried out. The 4 main soil types found in the areas investigated were nominally outlined in the NMDS-plots (based on site typology, see Table 1).

Using the commercially available XRD peak analysis software, XPowder (available at http://www.xpowder.com/), relative abundances of component minerals in rocks and soils were modelled as mixtures of 8 reference minerals common to ultramafic rocks using a reference intensity ratio approach. The samples studied here were considered mixtures of the following minerals: diopside (a pyroxene, PDF 016581), tremolite (an actinolite-type amphibole, PDF 011983), antigorite (a serpentine variety, PDF 018242), lizardite (a low temperature serpentine variety, PDF 015238), forsterite (Mg-rich olivine, PDF 023357), spinels (representing spinel group minerals including magnetite, PDF 018254), talc (PDF 019690) and montmorillonite (a smectitic clay mineral, PDF 012866). Modelled proportions of these minerals should be considered estimates, given, for example, that spinel and magnetite are binned under "spinels," and that multiple clay minerals share the 14 to 16 Å peak characteristic of smectite group clays, etc. Given that the same modelling strategy was applied across all samples, relative differences in major minerals can be observed in the results. Of course, modelling only provides an incomplete description of the mineralogy and should interpreted with caution.

Results

Bedrock elemental chemistry and mineralogy

Summarised chemistry of ultramafic bedrock samples (n = 76) is given in Table 2. These analyses are compared with samples from non- ultramafic bedrock from Kinabalu Park and nearby Mount Trus Madi (n = 13). Mean concentrations of Ca, Co, Cr, Cu, Fe, Mg, Mn, Ni and Zn are all markedly higher in ultramafic rock than in non-ultramafic rock samples, whereas K, Na, P and Si are higher in non-ultramafic rock. Compared to the protolith initial concentrations, the elements Al, Ca, Mg, Co, Ni and Zn are significantly enriched during weathering and soil formation. X-ray Diffraction analyses of rock samples show that minerals such as olivines (forsterite), pyroxenes (diopside, enstatite), amphibole, and spinels (chromite, magnetite) characterize the mineralogy of the peridotite bedrock (Fig. 2). All ultramafic rocks present in the Kinabalu Park area are serpentinised to varying degrees, however, the more serpentinised samples also contain talc, chlorite, and magnetite as minerals in addition to serpentines, olivines and pyroxenes.

Soil elemental chemistry

Table 3 presents summarised bulk chemistry of ultramafic soils, contrasted with non-ultramafic soils. Mean pseudo-total concentrations of Al and P were roughly similar among soils, whereas concentrations of Ca, Co, Cr, Fe, Mg, Mn and Ni were unsurprisingly much higher in ultramafic soils. On the other hand, pseudo-total concentrations of K were higher in non- ultramafic soils. The mean DTPA-extractable trace elements (Co, Cr, Cu, Ni and Zn) were all higher in ultramafic soils, except for Fe, which is similar. Potentially plant-available P (Mehlich-3 extract) was more than four times higher in average in non-ultramafic soils than in ultramafic soils (mean 12 vs. 2.7 $\mu g\ g^{-1}$). The soil pH range was 3.5 to 9.7 for all soils. Generally, the ultramafic soils were less acidic than the non-ultramafic soils with a mean pH of 6.0 as opposed to the much lower value of 4.6 for non-ultramafic soils. However, there was a wider range of pH values among ultramafic soils than among non-ultramafic soils: ultramafic laterites display acidic pH values as on non-ultramafic substrates whereas soils on serpentinite have unusually high pH values (see Table 4). Mean exchangeable Ca, Mg and Na were much higher in ultramafic soils, and exchangeable K was similar be- tween ultramafic and non-ultramafic soils (Table 3). Mean exchangeable Al was much higher in non-ultramafic soils. The Mg:Ca in the exchangeable complex was always < 1 in non-ultramafic soils (mean is 0.2) and > 1 (mean is 5.3) in ultramafic soils. Exchangeable K was very low and exchangeable Mg was relatively high, and the Mg:Ca molar quotient in some soils is extremely high (up to 82). Consequently, the electrical conductivity (EC) was also higher in ultramafic soils than in non-ultramafic soils. Soil pseudo-total elements of the main 'ultramafic edaphic islands' are shown in Table 4, whereas soil extractable trace elements, exchangeable macro-elements are shown in Table 5.

Soil mineralogy and pedological markers in selected profiles

Among soils, we observed several features of mineralogy and pedogenic indices of selected profiles (Figs. 2 & 3, Tables 6 & 7). Firstly, Hypereutric Leptosols displayed horizons that were highly serpentine- rich, with a limited smectite component, and also contained primary magnetite. In Eutric Cambisols (Hypermagnesic), some of the primary minerals were still substantially present in the BW horizons. In these soils (e.g. Cambisols at Tambuyukon summit), we observed a mixture of primary silicate minerals (amphiboles, pyroxenes and talc) and secondary Fe oxihydroxides (goethite). In more developed Geric Ferralsols, no trace of primary minerals could be found except spinels (i.e. magnetite and chromite). The mineralogy of B lateritic horizons (i.e. ferralic horizon) was dominated by goethite (e.g. Serinsim). Pisolithes can be found at the surface of such soil profiles that usually derived from crystallisation and dehydration of oxihydroxides. General features of all soil profiles but Leptosols included relatively acidic surface horizons with a marked increase in soil pH and in Mg:Ca ratios with a depth (Table 8). This rise in pH (and CEC) coincides with the increase in exchangeable Mg and Ca ions. Along with pH and CEC saturation increase was the increase of the Mg:Ca ratio with depth. Calcium was better retained by the CEC than Mg in A and B horizons of Ferralsols. In the hypermagnesian Leptosols, no such differentiation was observed and surface CEC was saturated by Mg.

Metal bearing-phases and availability in soils

The sequential extraction (Fig. 4) showed that amorphous Fe-oxides ('AM-Fe') were important phases for Ni and Cr in Eutric and Dystric Cambisols, but not in Geric Ferralsols where crystalline Fe-oxides ('CR- Fe') were by far the dominating fraction of Fe-oxides. In all soils, exchangeable Cr was extremely low (not visible on the graph), whereas exchangeable Ni in Hypereutric and Dystric Cambisols was relatively high (up to several % of total Ni). In contrast, exchangeable Co was extremely high in some Geric Ferralsols, but not in Hypereutric Leptosols. Residual concentrations for all four elements made up >50% of the total partitioning although many studies report incomplete dis- solution of crystalline Fe-oxides with one single DCB extraction (Becquer et al., 2006).

The carboxylic acid extractable Co was extremely high in the Eutric Cambisols Hypermagnesic with up to 122–263 $\mu g\ g^{-1}$ (on Mount Tambuyukon), whereas extremely high extractable Ni occurred in both Eutric Cambisols Hypermagnesic on Mount Tambuyukon (176–404 $\mu g\ g^{-1}$) and in Leptosols (Hypermagnesic) at Wuluh River (240–414 $\mu g\ g^{-1}$). Pseudo-total Mn concentrations were highest in Dystric Cambisols and Cambisols (Hypermagnesic) in the high-altitude zone of Mount Tambuyukon, reaching up to 33,590 $\mu g\ g^{-1}$, probably because of humid conditions prevailing in these soils (due to the altitude). The carboxylic acid extractable Mn was also extremely high in these soils (up to 3727 $\mu g\ g^{-1}$). Likewise, pseudo-total and carboxylic acid extractable Ni were similarly extremely high (up to 7000 $\mu g\ g^{-1}$and 404 $\mu g\ g^{-1}$ respectively) at this location and likely to contribute to the toxicity of these soils. High pseudo-total Cu occurred on a variety of soils reaching up to 453 $\mu g\ g^{-1}$, but extractable concentrations were low in all soils.

Soil discrimination according to geochemical properties

Fig. 5 shows two NMDS-plots of pseudo-total elements (top panel) and exchangeable and extractable elements (bottom panel) with the 13 different sites coloured-coded (and non-ultramafic comparison soils included). In the NMDS (Fig. 5), the two major sets of opposing vectors were Mg, Na, Ca and Fe, Cr, with the Hypereutric Leptosols (4) clustering along the first, and the Geric Ferralsols (1) clustering along the far end of the second. The (Hyper)Eutric Cambisols (3) spread towards the Fe, Cr vector, and the Dystric Cambisols (2) were intermediate. The non-ultramafic comparison soils clustered towards the K and Al vectors, probably because of the scarcity of these two elements in ultramafic soils. The NMDS with extractable and exchangeable elements was very different, and only the Eutric Cambisols were immediately apparent towards the exchangeable Mg, Ca vector. The Eutric Cambisols clustered towards the carboxylic acid extractable Fe, Mn, Ni vector. The Dystric Cambisols were intermediate, whereas the Ferralsols clustered in the centre, which can be explained by extremely low extractable/ exchangeable elements as a result of intensive leaching. The soils from Marai Parai are waterlogged and have extremely high exchangeable Al, similar to many of the sandstone-derived non-ultramafic soils. The soils from Bukit Hampuan, Bambangan and Mesilau, all localities with complex geologies that contain serpentinite bedrock, evident in bedrock analysis and in the vegetation, cluster towards the exchangeable Mg, Ca vector.

Discussion

Characteristics and distribution of the main ultramafic soil types

The characteristics of the (Hyper)Eutric Cambisols (Hypermagnesic) with extremely high Mg:Ca molar quotients and very high extractable Ni and Mn concentrations results from direct and moderate weathering of the bedrock with still many primary minerals, and hence the soil chemistry is largely a reflection of that bedrock. These soils are shallow and boulders of bedrock dominate the surface with limited signs of soil formation processes, although mineral weathering shows evident signs of the formation of a Cambic horizon with a stable complex. Also, Ni release through mineral dissolution and its uptake by neo-formed high CEC clays and poorly crystallised Fe oxides, are favourable to its high availability (Massoura et al., 2006; Chardot et al., 2007; Echevarria, 2018). In these soils, Mg:Ca can be as high as 70, which is highly unbalanced. They are mainly found at Layang-Layang (high-altitude Mount Kinabalu) and in the summit zone of Mount Tambuyukon. These shallow soils present multiple toxicities; extremely high phytoavailable Ni, Co and Mn and extremely high exchangeable Mg (and high Mg:Ca quotients) that are similar to those found in the ultramafic soils of the temperate and Mediterranean regions (Chardot et al., 2007; Bani et al., 2014) but also in ultramafic Eutric Cambisols from tropical regions (Borhidi, 1988; Proctor, 2003). Under such peculiar geochemical conditions the vegetation ranges from stunted upper montane forest (9–10 m) to tufts of dwarf-scrub barely 0.3 m tall. Although in the cloud-zone, high wind velocity coupled with high altitude causes this habitat to have great temperature and moisture regime extremes. Similar soils occur in the summit zone of Mount Tambuyukon (2300–2570 m), and here a unique (species-rich) graminoid scrub with many endemics has evolved despite the soils having such high Mg:Ca quotients and phytoavailable Ni and Mn. Therefore, altitude plays a significant role in the ultramafic stress that soils exert on the vegetation. The most common soils in Kinabalu Park are montane Cambisols (Dystric Cambisols) that occur on moderate to steep slopes at altitudes of 900–2500 m. Particularly in the cloud forest zone, there is a thick build-up of mor humus at the surface and in some flatter and wetter areas, sphagnum peat. The typical vegetation is either open lower montane forest (> 1800 m) or dense upper montane forest (‘cloud forest’) at altitudes 1800–2500 m. These soils are acidic (pH 4.5–5.8) with low CEC and intermediate Mg:Ca quotients. These soils are very widespread in Kinabalu Park and cover most (steep slopes) of ultramafic bedrock outcrops. The formation of peat on shoulders has been attributed to the frequency of cloud-cover and hence the continuous saturation of the soil (Proctor et al., 1988). These ultramafic soils are fairly similar to the non-ultramafic soils at the same altitude and, as a consequence, few plant species are unique to the ultramafic equivalents, although stunting is more pronounced, probably due to the relatively high Mg:Ca, low K and P contents, and high Ni availability (Borhidi, 1988; Proctor et al., 1999). The ultramafic soils at Marai Parai (1550–1700 m) on Mount Kinabalu's west face are constantly waterlogged from water percolating from the granite summit plateau that towers above. As a result, there is peat formation and acidification of these soils and the vegetation is a graminoid scrub resembling that of the summit region of Mount Tambuyukon at much higher altitude, despite entirely different soil chemistries. They likely resemble the “sols à accumulation humifères” described in New Caledonia> 900 m in many ways, including the low pH (Latham, 1975a). The lack of trees might be explained by the combination of waterlogging and extremely high concentrations of exchangeable Al that are likely to be phytotoxic at pH below 5.2.

Finally, deep laterite soils (Geric Ferralsols) occur in low-lying areas in valleys and on plateaus where flat surfaces occur which allow for these old and intensively weathered soils to occur (Echevarria, 2018). Although not widespread in the mountainous terrain of Kinabalu Park, these types of ultramafic soils are common elsewhere in Sabah, and also in many other tropical settings (Latham, 1975b; Becquer et al., 2001; Proctor, 2003; Garnier et al., 2009), and are particularly well developed on the Mount Tavai Plateau near Telupid. These are 'lateritic' red deep soils (up to 36 m has been observed at a road excavation), well-drained and frequently have marked iron concretions (ferricrete: plinthic or petroplinthic surface horizons) on the surface. Pseudo-total concentrations of Fe and Cr are extremely high, CEC is very low, 2:1 clay minerals are absent from the soil profiles, and concentrations of extractable (i.e. plant-available) trace elements (Ni, Co, Cr) are all low. The Mg:Ca quotient is generally low due to long and intense weathering which completely leaches Mg out, but not Ca. These soils are not likely to have major effects on the vegetation and do not show additional geochemical stress than in other laterites formed on non-ultramafic materials. Only the presence of available Cr-VI amounts in ultramafic laterites may have some effect on the biota, but this has not been documented (Garnier et al., 2009). The vegetation on these soils (particularly on undulating terrain and plateaux) is tall dipterocarp-forest with a sparse understorey of tree saplings but virtually no herbs. Despite very low concentrations of (plant-available) nutrients, including P, Ca and K, these soils support high biomass ecosystems. Most nutrients are contained in the living biomass, and recycling from leaf litter mass is fast (as evidenced by the distinct absence of any significant leaf litter accumulation) and efficient (as indicated by the high densities of surface roots). Geric Ferralsols are the most benign in terms of their chemical properties, notwithstanding they are (very) nutrient-poor although that in itself is not unique, as (lowland) rainforests (on non-ultramafic Ferralsols) soils are generally nutrient-poor (Whitmore, 1975; Vitousek and Sanford, 1986), Experimental work on these ultramafic rainforest soils has shown that nutrient-limitation rather than toxicity is likely important here (Proctor et al., 1999; Brearley, 2005).

The three major serpentinite occurrences in Kinabalu Park are located in the Wuluh Valley, the Bambangan Valley and the Panataran Valley. At these locations, rivers cut through the formations, which originally formed along major fault lines (and such topographic weaknesses are exploited by the rivers in the present day). These fault lines were fissures during emplacement through which water could circulate and interact with peridotite rock resulting in serpentinisation. Serpentinitic soils occur mainly on (extremely) steep slopes facing the respective rivers. At these localities, massive serpentinite bedrock crops out and is undercut by a river, causing cascades of landslides of fresh rock debris. The unweathered debris is rich in fine particles including mostly clay minerals (talc, smectite) but these soils have very shallow development and little weathering features, which classifies them as Hypereutric Leptosols (Hypermagnesic), the least developed ultramafic soils of all. They usually develop on< 20 cm and lack a BW horizon. The older soils on ridges and old landslides have a thicker layer of organic matter (O-horizon) mainly made up of 'needles' of Ceuthostoma sp. (Casuarinaceae) trees which decompose slowly, with a developed A1-horizon (< 20 cm) and unaltered serpentinite debris underneath (C horizon). The soil pH ranges from 6.5 in the soils rich in organic matter to pH 9.8 in the unweathered soil (C horizon and further down the profile (> 50 cm), which are extreme values for soils, comparable to those of saline soils. Some of these serpentinitic Hypereutric Leptosols have extremely high carboxylic acid extractable Cr concentrations. The high phytoavailable Cr concentrations in these soils are mostly due to Cr-VI that is formed during Mn oxide reduction in the clay-dominated horizons of tropical ultramafic soils (Garnier et al., 2009; Raous et al., 2013). Such available Cr-VI concentrations could produce toxic effects on the vegetation, but this has not been studied. Some mixed soil types also exist, in particular Bambangan and Mesilau (moderately deep montane soils with mor humus build-up overlying on serpentinite bedrock), and Bukit Hampuan (also serpentinite bedrock, but drier eroded soils). The intermediate properties of these soils are reflected in their soil chemistry (relatively high pH, high Mg:Ca) as well as in the vegetation these soils support (frequent occurrence of Ceuthostoma sp. – Casuarinaceae – indicative of serpentinite and high pH). All four types are clearly distinguished by statistical analyses, which underlines their significance in terms of soil classification and later on for the interpretation of soil-vegetation relationships. In comparison with other tropical ultramafic soils from around the world (Table 9), the ultramafic soils from Kinabalu Park are diverse in their chemical properties, and some of the extractable concentrations of Ni, Co and Cr that were recorded are exceptionally high. They usually show broader ranges of all parameters than other reported sites, except for total Ni (see data for Brazil). In particular, the existence of soils with strongly alkaline pH (i.e. Hypereutric Leptosols) is not reported elsewhere in tropical ultramafic regions. Although extractable Cr was highest in Hypereutric Leptosols, pseudo-total Cr was highest in Geric Ferralsols (at the Serinsim site) and comparable to the very high values found in New Caledonian or Brazilian soils.

Effects of bedrock serpentinisation and weathering on soil types

In the literature, soils derived from either peridotite or serpentinite bedrock are often called 'serpentine soils' and botanists and ecologists commonly do not distinguish between these two types (as emphasised by Alexander, 2004, 2009). Although arguments have been made to term 'serpentine soils' more generally 'ultramafic soils', which is geo- logically correct and avoids confusion with 'serpentinite', the term is cemented in the field and in literature (Brooks, 1987). The differences between soils derived from 'peridotite' and 'serpentinite' are ecologically important, but they form a complex matrix of soil pedological and chemical properties that depend on weathering, altitude and topography (Jaffré, 1980; Proctor et al., 1999; Kierczak et al., 2016; Echevarria, 2018). It was hypothesized that soils derived from bedrock with a higher degree of serpentinisation result in soil chemistries with more adverse properties to plant life (Kierczak et al., 2016; Echevarria, 2018). Two types of soils turned out to have extreme chemical properties however: (i) soils derived from peridotite at high altitude – (Hyper)Eutric Cambisols (Hypermagnesic) – where rejuvenation through erosion maintains soils at an early weathering stage (Echevarria, 2018), and (ii) soils derived from strongly serpentinised bedrock – serpentinitic Hypereutric Leptosols (Hypermagnesic) – whose evolution is slow because of their unusual mineralogical composition (i.e. dominated by slowly-weathered serpentine and talc minerals).

Fully developed laterites (Geric Ferralsols) show much lesser influence of the original ultramafic material. For instance, pH values, exchangeable Ca over exchangeable Mg, exchangeable Ni are more similar to other Ferralsols developed on non-ultramafic materials. In Ferralsols, Ni is hosted mainly by crystallised Fe-oxides and the resulting availability is extremely low (Becquer et al., 2006; Massoura et al., 2006; Raous et al., 2013). In contrast, Cr-VI available pool can be significantly elevated (> 1000 $\mu g\ g^{-1}$) also in these soils (Garnier et al., 2009; Raous et al., 2013) and may have an effect on the vegetation, but this has not been investigated.

How ultramafic soil diversity does influence floristic patterns?

Deep laterite soils (Geric Ferralsols) developed on undulating terrain, either over peridotite or strongly serpentinised peridotite, were characterised by extremely high pseudo-total Fe and Cr, low CEC (0.1–2 $cmol\ kg^{-1}$), acidic (pH 4.5–5.5) and low exchangeable Mg (but also low exchangeable Ca and K). Distribution: Serinsim, Nalumad. These deep ultramafic Geric Ferralsols support tall species-rich rainforest, not dissimilar to podzolised sandstone nutrient-poor forests elsewhere in Sabah, with the dipterocarps *Shorea laxa* and *Shorea venulosa* and the gymnosperm *Agathis borneensis* (Araucariaceae) dominating. Other characteristic dipterocarps include *Dipterocarpus lowii, D. ochraceus, Shorea kunstleri, S. laxa, S. lowii, S. tenuiramulosa, S. venulosa* and *Dryobalanops beccarii* (Acres et al., 1975; Ashton, 1982). Comparable rainforests growing on Geric Ferralsols at low altitude are found in the area of Moa in Cuba (Borhidi, 1988), on the alluvial soils of Rivière Bleue in New Caledonia (Jaffré, 1980, 1992; Isnard et al., 2016). Recurring fires may be involved in the lack of forest development on many tropical Ferralsols (Proctor, 2003), as in New Caledonia, where the rainforest is now limited to alluvial plains at low altitude (Isnard et al., 2016).

Moderately deep montane soils (Dystric Cambisols) frequently with high build-up of organic matter (mor humus) are acidic (pH 5–6), have with high exchangeable Al, but low CEC (1–3 cmol kg^{-1}) and high pseudo-total Fe, Cr and Ni. Distribution: Mesilau, Bukit Babi, Bambangan, Marai Parai, Bukit Hampuan, Mount Tambuyukon (slopes), Mount Nambuyukon. The Dystric Cambisols are the most widespread soils in the 'cloud-forest' zone of Kinabalu Park. The tree density is generally high and these ecosystems have high species diversity, particularly in epiphytes such as orchids. The vegetation is typical for this altitudinal zone, and dominated by trees in the families Myrtaceae, Fagaceae, Podocarpaceae and Rubiaceae. The vegetation, however, differs little from soils derived from non-ultramafic bedrock in the same area, although physiognomy is often more stunted on the ultramafic soils for reasons not fully understood. Strongly serpentinised soils on high altitude (Bukit Hampuan, Bambangan, Mesilau) have Dystric Cambisols, but these are much more base-rich (CEC, pH) and have higher Mg:Ca quotients compared to peridotite-derived ultramafic soils or non-ultramafic soils, which is reflected in species-rich vegetation.

Shallow skeletal soils on high-altitude (2400–2950 m) weathered peridotite with little organic matter (Eutric/Hypereutric Cambisols Hypermagnesic). These soils are young and rejuvenated by erosion and are characterised by high pseudo-total and exchangeable Mg, low CEC (3–5 cmol kg^{-1}), high extractable Ni (50–180 µg g^{-1} DTPA-Ni) and Mn (250–500 µg g^{-1} DTPA-Mn), and are moderately acidic (pH 5–5.8). Distribution: Mount Tambuyukon (summit), Layang-Layang. The skeletal Eutric Cambisols are extreme in their chemical properties (high Mg:Ca, high extractable Ni and Mn), and coupled with high altitude (2400–2950 m) have given rise to very stunted vegetation dominated by species in the Myrtaceae and Podocarpaceae at Layang-Layang on Mount Kinabalu's south slope. On the more exposed slopes, the vegetation is co-dominated by just two plant species, *Leptospermum recurvum* (Myrtaceae) and *Dacrydium gibbsiae* (Podocarpaceae), both endemic. Locally, the carnivorous pitcher plant *Nepenthes villosa* (Nepenthaceae), also endemic, is common. The ultramafic graminoid vegetation (< 1 m high) on the exposed summit ridges of Mount Tambuyukon is unique and not found anywhere else in Sabah or Borneo. This vegetation type is characterised by a range of shrubs such as *Tristaniopsis elliptica* (Myrtaceae), *Lithocarpus rigidus* (Fagaceae), *Ternstroemia lowii* (Pentaphylacaceae), Scaveola verticillata (Goodeniaceae), *Wikstroemia indica* (Thymelaeaceae), *Leptospermum recurvum* (Myrtaceae), *Podocarpus brevifolius* and *Dacrydium gibbsiae* (Podocarpaceae), the sedges, *Gahnia javanica* and *Schoenus melanostachys*.

Soils developed on bare serpentinite (serpentinitic hypermagnesic Leptosols) at low altitude (400–700 m) have high total and exchangeable Mg (Mg:Ca 5–25), very high CEC (15–25 cmol kg^{-1}), high extractable Ni (20–50 µg g^{-1} DTPA Ni) and circum-neutral pH (6.5–7.5) near the surface and highly alkaline at depth (pH 8–9.5). Distribution: Panataran Valley, Wuluh River. The serpentinitic Leptosols give rise to a mosaic of landslides, with the older landslides and the ridges having open medium-tall forest dominated by Casuarinaceae (*Gymnostoma sumatranum*, *G. nobile* and *Ceuthostoma terminale*) whereas the younger landslides have pioneer communities often with shrubs of *Scaevola micrantha* (Goodeniaceae), *Decaspermum vitis-idaea* (Myrtaceae) and *Macaranga kinabaluensis* (Euphorbiaceae). Two terrestrial hyper-endemic orchids, *Paphiopedilum rothschildianum* and *P. dayanum*, are restricted to this pioneer vegetation. Another hyper-endemic, the tree *Borneodendron aenigmaticum* (Euphorbiaceae), co-occurs with Casurinaceae in more developed forest. It is difficult to compare these soils with other regions in the world because of the local biodiversity features. However, in the region of Moa in Cuba, these soil types (Cambic Leptosols or Hypereutric Leptic Cambisols) are those with the highest level of endemism (Borhidi, 1988). In New Caledonia, maquis on Magnesic Cambisols also hosts high diversity and levels of endemism (Isnard et al., 2016). It is also where the greatest physiological stress (e.g. water stress and sclerophyllous adaptation) have been reported (Isnard et al., 2016). Therefore, these soils in particular host the most highly adapted plants from ultramafic tropical regions due to the high constraints they exert on plant physiology. It is possible that the adapted Casuarinaceae from Sabah display specific adaptation to the geochemical constraints that these soils represent.

Numerous experimental studies have demonstrated Ni toxicity in plants in ultramafic soils (for example L'Huillier and Edighoffer, 1996; Kukier and Chaney, 2001), but some rare plant species actually thrive in Ni-rich soils. These plants, nickel hyperaccumulator species, plants that sequester in excess of 1000 $\mu g\ g^{-1}$ Ni in their shoots (van der Ent et al., 2013) are also known from Sabah (Proctor et al., 1988; Van der Ent et al., 2016b). Their occurrence in Sabah (van der Ent et al., 2016a) is restricted to soils with exceptionally high available Ni, mainly strongly serpentinised soils in the lowlands (<1200 m asl). These occurrences are localized on very shallow soils with active mineral weathering. In such soils, the dissolution of primary minerals releases Ni, which is then made available by adsorption onto high CEC clays and non-crystallised Fe-oxides. This allow Ni exchangeable pools to be high enough to favour Ni hyperaccumulation by specialised species, for ex- ample in Nalumad where the strongly serpentinised soils also have high pseudo-total Mn (8698–16,120 $\mu g\ g^{-1}$) and up to 300 $\mu g\ g^{-1}$ DTPA- Mn and 276–654 $\mu g\ g^{-1}$ DTPA-Cr. The occurrence of Ni-hyper- accumulators in ultramafic areas of Sabah has been shown to be strictly correlated with high-Mg soils and has not been reported on laterites (van der Ent et al., 2016a). Manganese hyperaccumulation is also re- ported in Magnesic Cambisols in New Caledonia because of the specific conditions for Mn mobility in these soils (Isnard et al., 2016). This could be investigated as well on the ultramafic Cambisols of Sabah.

Finally, as reported in other studies from other tropical ultramafic regions of the world, the floristic zonation with altitude is more pronounced on ultramafic substrates than on non-ultramafic substrates, for example in Cuba (Borhidi, 1988), and on Mount Silam in Sabah (Proctor, 2003). This may be explained due to the geochemistry of the soils (altitude soils are mostly Dystric or Hypereutric Cambisols because the slope rejuvenates the profile).

Conclusions

The occurrence and chemical characteristics of these soils are a function of bedrock mineralogy (serpentinisation), weathering and landscapes attributes (altitude, slope). Overall, ultramafic soils are less acidic, have higher EC, higher pseudo-total Ca, Co, Cr, Fe, Mg, Mn and Ni, higher exchangeable Ca and Mg, higher Mg:Ca quotients, similar exchangeable K, higher DTPA-extractable Co, Cr, Cu and Ni, and lower chemically-extractable P than adjacent non-ultramafic soils. Well-developed Geric Ferralsols probably show less differences from non-ultramafic soils under similar conditions than high altitude soils or shallow erosion-rejuvenated Cambisols. Therefore, they host ecosystems that show little difference with those present in soils developed on other types of bedrocks. On the contrary, ultramafic Leptosols or shallow hypermagnesic Cambisols that form on serpentinite substrates host specific and adapted vegetation (high levels of endemism) that tolerates geochemical peculiarities, including Ni hyperaccumulators. This is also reported for other ultramafic tropical outcrops (e.g. Cuba, New Caledonia, Philippines). Whether soils are moderately or weakly weathered due to the original mineralogy (i.e. strongly serpentinised bedrock) or due to lack of evolution (high-slope erosion/rejuvenation), the so-called ‘serpentine syndrome’ only seems to be restricted to these two types of soils. However, the geochemical Cr anomaly (i.e. high levels of exchangeable Cr-VI) of ultramafic laterites may exert effects on the vegetation, but this has not been studied. The highest level of edaphic stress is concentrated on fully serpentinised ultramafic outcrops, which should be prioritised areas for the search for endemic plants on ultramafic substrates in Sabah and other tropical regions.

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FIGURES AND TABLES

Fig. 1. a. Shaded relief map of Sabah with major ultramafic occurrences (marked in red) totalling approximately 3500 km^2 (van der Ent et al., 2014). b. Geological map of the study area with sampling sites marked (coloured circles). Geology shape files from Robert Hall, Department of Earth Sciences, SE Asia Research Group, Royal Holloway, University of London.

Fig. 2. Stacked XRD profiles for rock specimens, with diagnostic peaks and Miller indices provided for constituent minerals. ACT =actinolite (here tremolite – an amphibole), ENST = enstatite (a pyroxene), DIOP = diopside (a pyroxene), FOR = forsterite (Mg-rich olivine), MAG= magnetite, SERP= serpentine, SPIN =spinel, TALC as written.

Fig. 3. Stacked XRD profiles for soil samples with diagnostic peaks and Miller indices provided for constituent minerals. ACT= actinolite (here tremolite – an amphibole), ENST = enstatite (a pyroxene), DIOP = diopside (a pyroxene), FOR =forsterite (Mg-rich olivine), MAG =magnetite, SERP= serpentine, SPIN =spinel, TALC, GOE =goethite, CHL = chlorite, and QTZ= quartz as written.

Fig. 4. Partitioning of Ni, Cr, Co and Mn over soil fractions (as percentage of total) of the four main soil types (EX= water soluble and exchangeable, Mn-OX = bound to Mn oxides, AMFe= bound to amorphous Fe oxides, CR-Fe, bound to crystalline Fe oxides, Res =residual).

Fig. 5. NMDS of pseudo-total soil elements (top panel) and exchangeable and extractable elements (bottom panel) from all collection sites, contrasted with non-ultramafic comparison soils. The 4 main soil types are nominally outlined in the NMDS-plots (based on site typology).

Table 1 Collection localities with environmental and pedological attributes (bedrock types, soil classes, soil depth).

Table 2 Bedrock chemistry (ranges and means) of ultramafic and non-ultramafic bedrock total values (pressurised HF/HCl/HNO_3 microwave digest).

Table 3 Chemistry of ultramafic and non-ultramafic soils. Abbreviations: 'pseudo-total' microwave-assisted digestion with HNO3 and HCl, 'DTPA' is DTPA-extractable metals, 'ML-3' is Mehlich-3 extractable P, and 'exch.' is exchangeable with silver-thiourea.

Table 4 Soil pseudo-total elements of the main 'ultramafic edaphic islands' in µg g^{-1} or mg g^{-1} if marked with asterisk (as means from unpressurised HNO3/HCl microwave digests).

Table 5 Soil extractable (carboxylic acid) elements (Co, Fe, Mn, Ni) in µg g^{-1}, exchangeable elements (Al, Ca, K, Mg, Na) in $cmol^{(+)}$ kg^{-1} and Mehlich-3 extractable P (µg g^{-1}), all as means.

Table 6 XRD modelled mineral relative abundances for selected rocks, assuming the sample is a mixture of crystalline diopside, tremolite (actinolite), antigorite, lizardite, spinel, talc, fosteritic olivine, and smectite group clay minerals. Total elemental concentrations in selected rock samples (µg g^{-1} or % if indicated).

Table 7 XRD modelled mineral relative abundances for selected soils, assuming the sample is a mixture of crystalline diopside, tremolite (actinolite), antigorite, lizardite, spinel, talc, fosteritic olivine, and smectite group clay minerals. Pseudo-total elemental concentrations in selected soil samples (μg g^{-1}). Elements that marked with asterisk are in mg g^{-1}.

Table 8 Soil profiles: pseudo-total values for soil in μg g^{-1} or mg g^{-1} (elements marked with asterisk) total values for bedrock in % (Ca, K, Mg, Al, Fe, Si) and μg g^{-1} (Co, Cr, Mn, Ni, P).

Table 9 Chemistry of tropical ultramafic soils from around the world.

FIGURE 1a

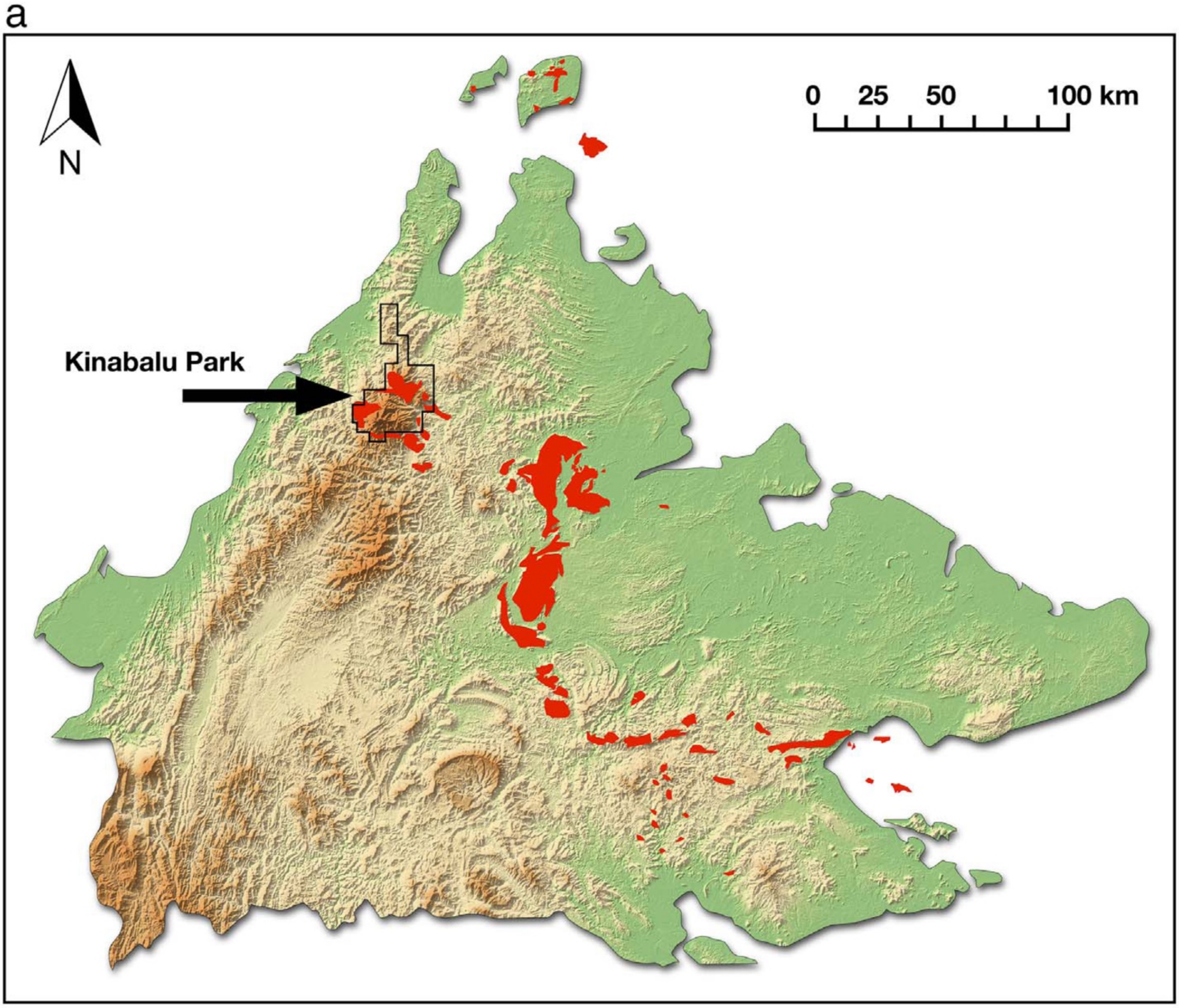


FIGURE 1b

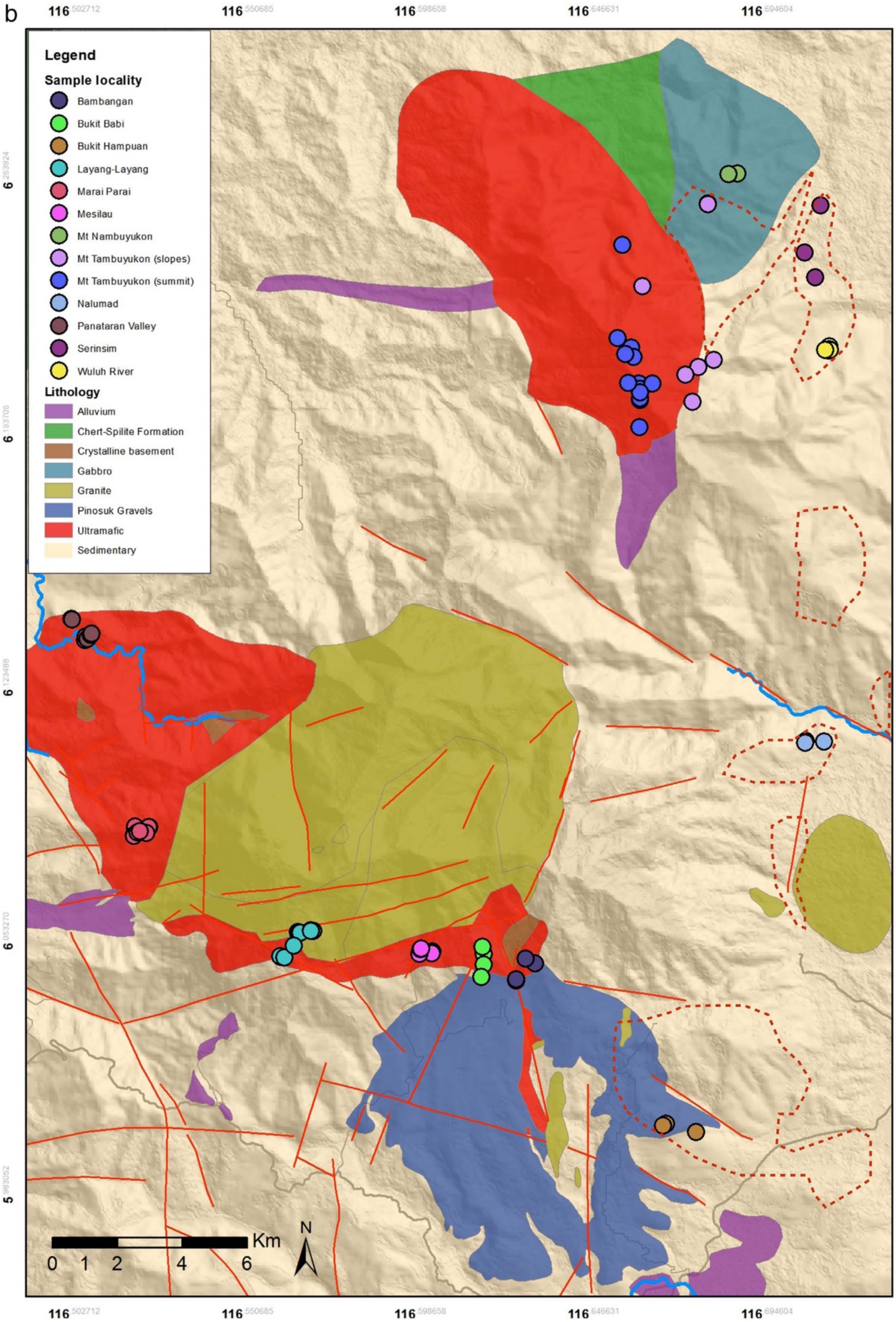

b
116 502712
116 550685
116 598658
116 646631
116 694604
Legend
Sample locality
Bambangan
Bukit Babi
Bukit Hampuan
Layang-Layang
Marai Parai
Mesilau
Mt Nambuyukon
Mt Tambuyukon (slopes)
Mt Tambuyukon (summit)
Nalumad
Panataran Valley
Serinsim
Wuluh River
Lithology
Alluvium
Chert-Spilite Formation
Crystalline basement
Gabbro
Granite
Pinosuk Gravels
Ultramafic
Sedimentary
Km
0 1 2 4 6
N

FIGURE 2

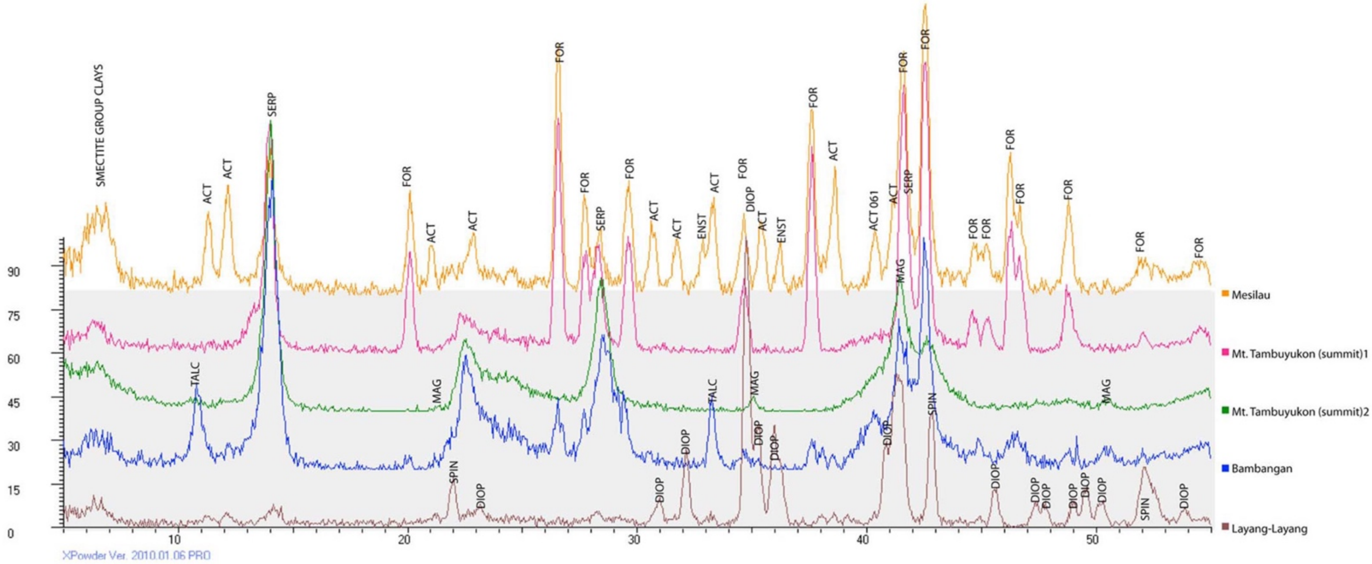
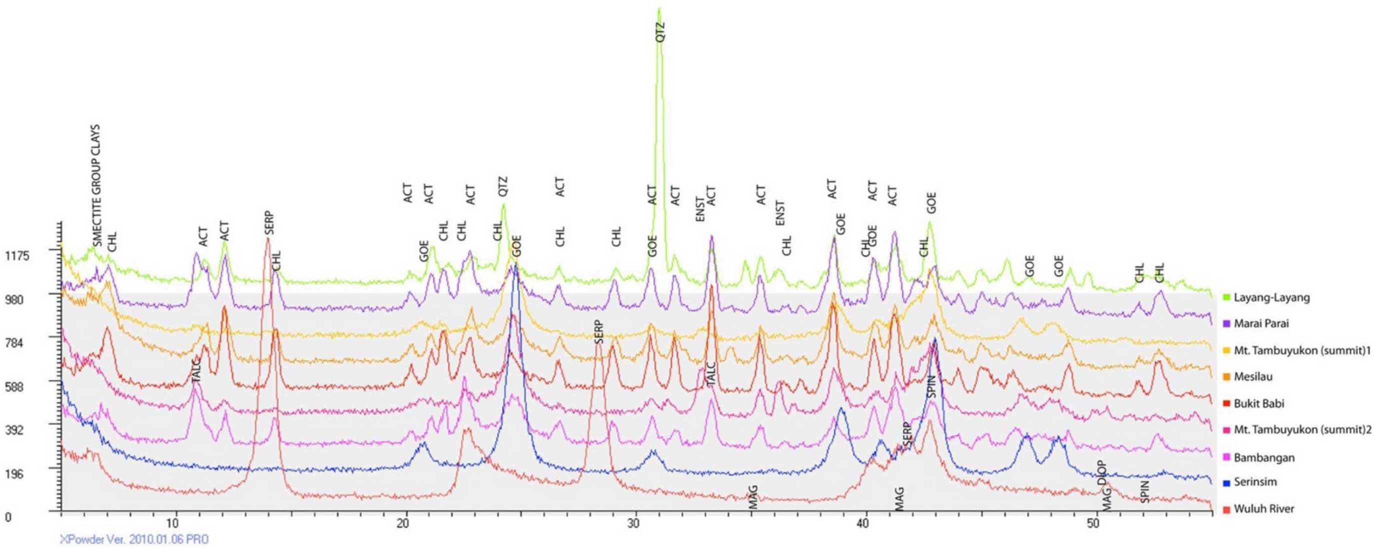
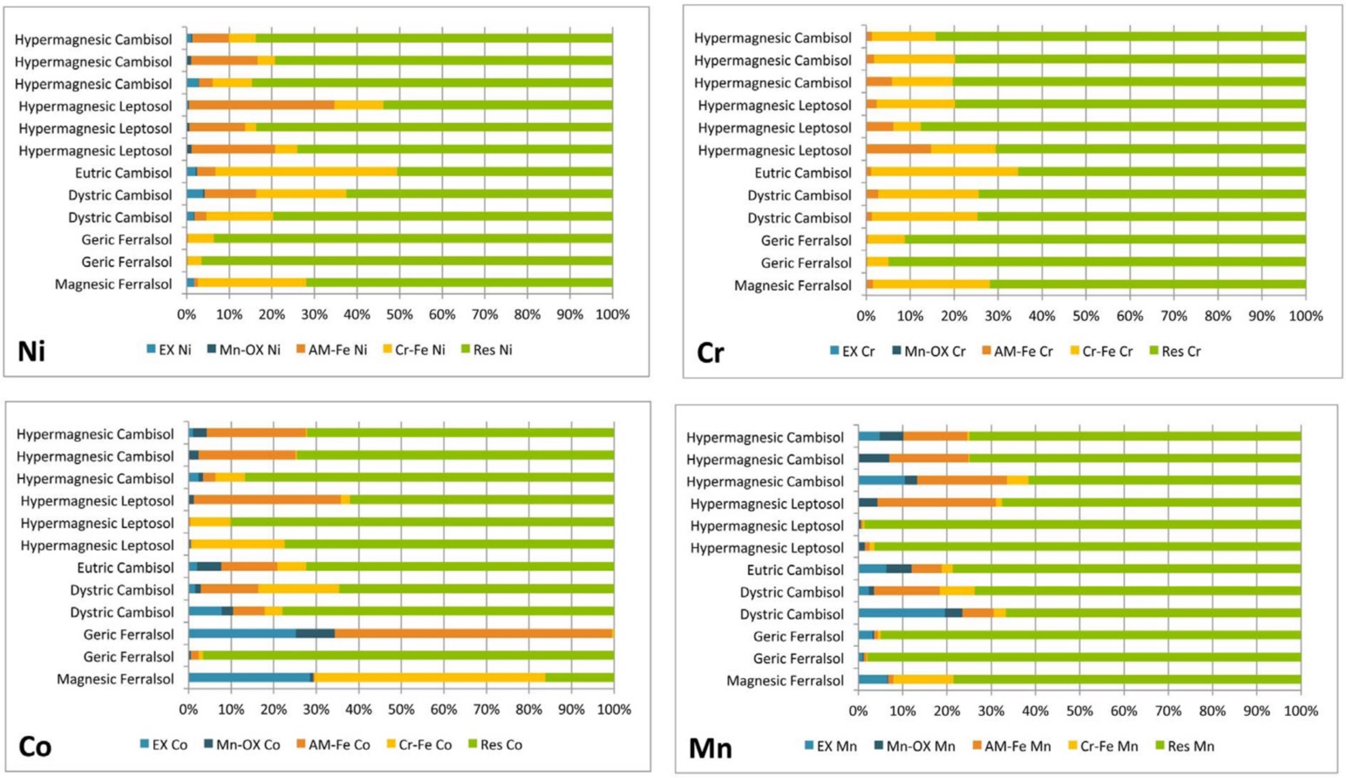

SMECTITE GROUP CLAYS
ACT
SERP
FOR
TALC
MAG
DIOP
ENST
SPIN
ACT 061
90
75
60
45
30
15
0
10
20
30
40
50
Mesilau
Mt. Tambuyukon (summit)1
Mt. Tambuyukon (summit)2
Bambangan
Layang-Layang
XPowder Ver. 2010.01.06 PRO

FIGURE 3



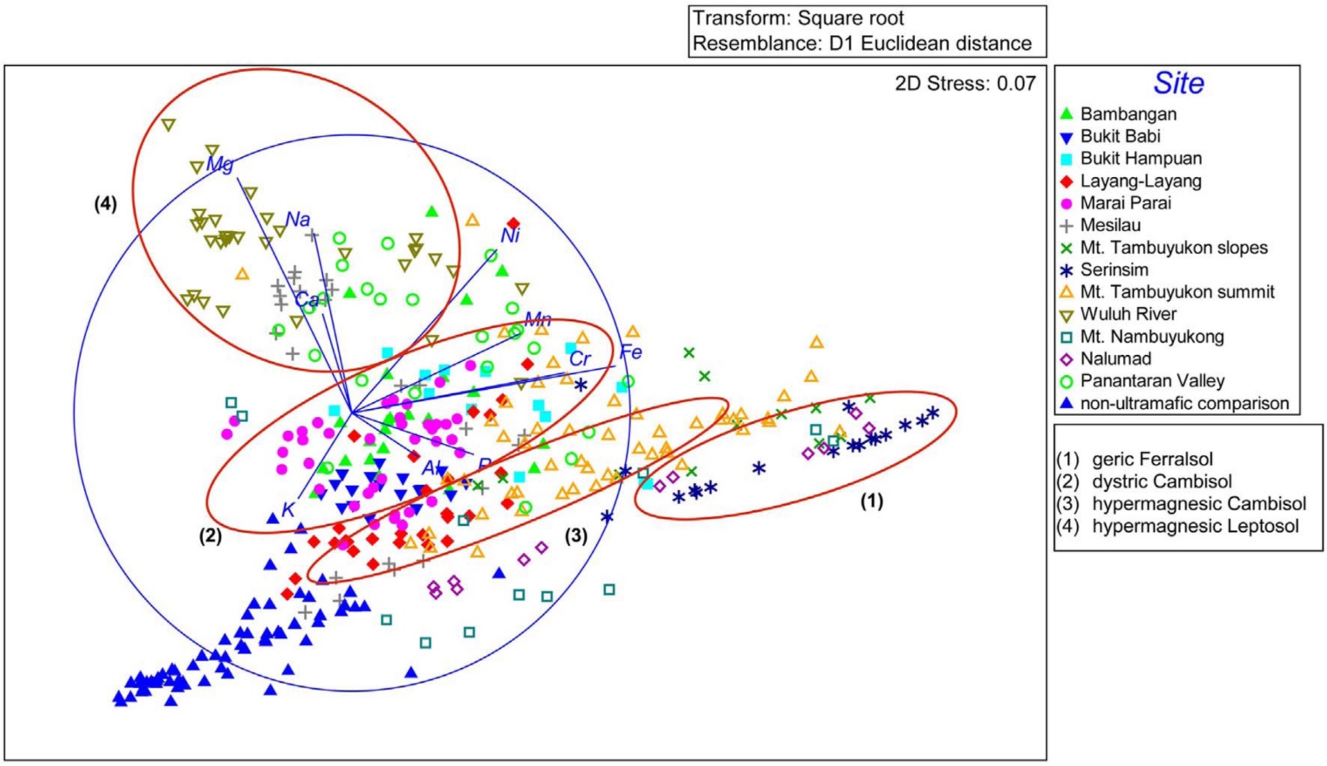
Layang-Layang
Marai Parai
Mt. Tambuyukon (summit)1
Mesilau
Bukit Babi
Mt. Tambuyukon (summit)2
Bambangan
Serinsim
Wuluh River
SMECTITE GROUP CLAYS
CHL
ACT
SERP
TALC
GOE
QTZ
ENST
MAG
SPIN
DIOP
1175
980
784
588
392
196
0
10
20
30
40
50
XPowder Ver. 2010.01.06 PRO

FIGURE 4

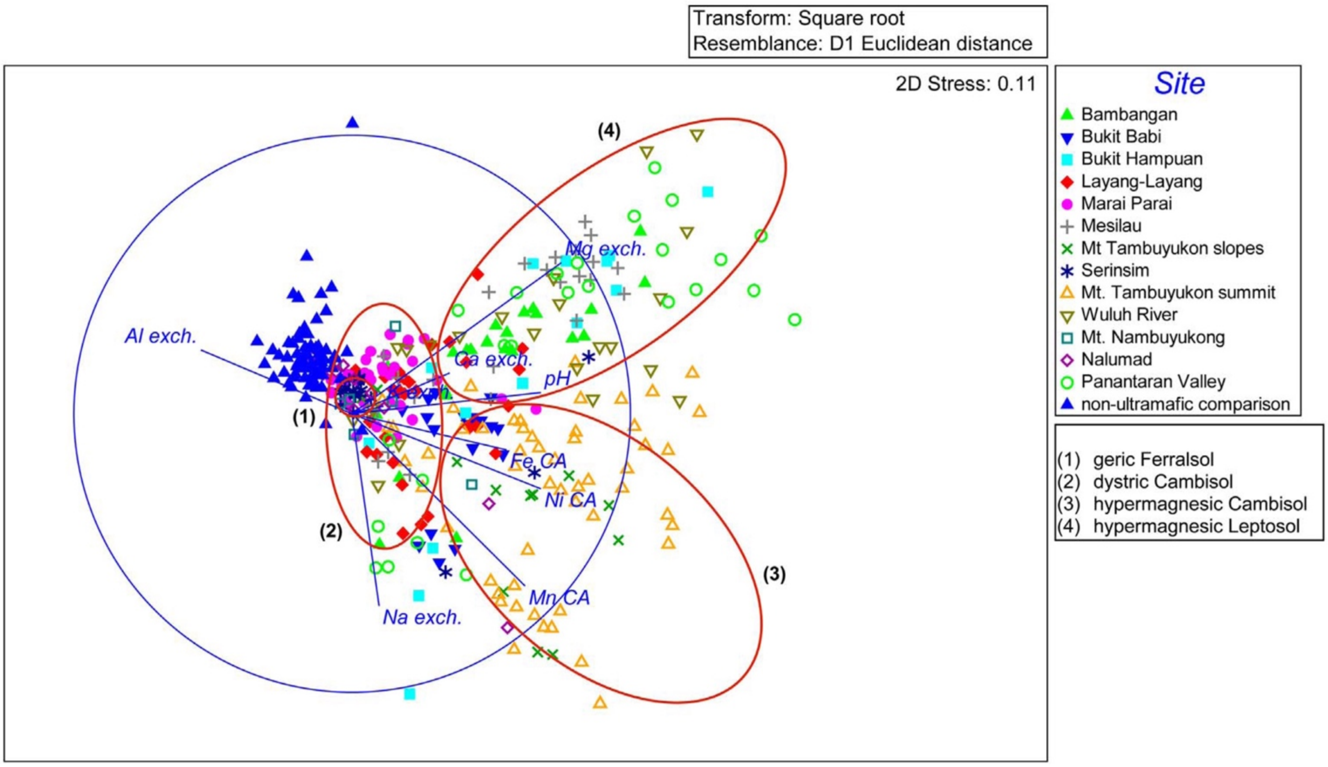


Hypermagnesic Cambisol
Hypermagnesic Leptosol
Eutric Cambisol
Dystric Cambisol
Geric Ferralsol
Magnesic Ferralsol
0% 10% 20% 30% 40% 50% 60% 70% 80% 90% 100%
Ni
EX Ni Mn-OX Ni AM-Fe Ni Cr-Fe Ni Res Ni
Cr
EX Cr Mn-OX Cr AM-Fe Cr Cr-Fe Cr Res Cr
Co
EX Co Mn-OX Co AM-Fe Co Cr-Fe Co Res Co
Mn
EX Mn Mn-OX Mn AM-Fe Mn Cr-Fe Mn Res Mn

FIGURE 5



Transform: Square root
Resemblance: D1 Euclidean distance
2D Stress: 0.07
Site
Bambangan
Bukit Babi
Bukit Hampuan
Layang-Layang
Marai Parai
Mesilau
Mt. Tambuyukon slopes
Serinsim
Mt. Tambuyukon summit
Wuluh River
Mt. Nambuyukong
Nalumad
Panantaran Valley
non-ultramafic comparison
(1) geric Ferralsol
(2) dystric Cambisol
(3) hypermagnesic Cambisol
(4) hypermagnesic Leptosol
Mg
Na
Ca
Ni
Mn
Cr
Fe
Al
P
K



Transform: Square root
Resemblance: D1 Euclidean distance
2D Stress: 0.11
Site
Bambangan
Bukit Babi
Bukit Hampuan
Layang-Layang
Marai Parai
Mesilau
Mt Tambuyukon slopes
Serinsim
Mt. Tambuyukon summit
Wuluh River
Mt. Nambuyukong
Nalumad
Panantaran Valley
non-ultramafic comparison
(1) geric Ferralsol
(2) dystric Cambisol
(3) hypermagnesic Cambisol
(4) hypermagnesic Leptosol
Mg exch.
Al exch.
Ca exch.
pH
Fe CA
Ni CA
Mn CA
Na exch.

TABLE 1

Site number	Locality	n (soils)	Altitude range (m asl)	Slope (%)	Bedrock type	Soil class	Soil depth (m)	O–A–horizon
1	Mt Tambuyukon (summit)	53	2318–2534	20–50	Peridotite (Dunite)	Eutric Leptic Cambisol (hypermagnesic)	< 0.3	Absent
2	Mt Tambuyukon (slopes)	12	1466–1906	< 20	Peridotite	Dystric Folic Cambisol (magnesic)	< 0.5	Mor accumulation
3	Wuluh River	35	750–820	50–75	Serpentinite	Mollic Leptosol (colluvic, hypermagnesic)	> 1	Thin A–horizon
4	Serinsim	15	612–671	< 20	Peridotite	Plinthic Geric Rhodic Ferralsol	> 5	Only leaf litter, iron concretions
5	Mt Nambuyukon	9	1584–1590	< 20	Serpentinite	Dystric Ferralic Cambisol	< 1	Thin A - horizon
6	Panataran Valley	26	588–781	20–50	Serpentinite	Mollic Leptosol (hypermagnesic)	> 1	Thin A - horizon
7	Marai Parai	34	2633–1753	< 20	Peridotite	Dystric Leptic Cambisol	< 0.3	Thin A - horizon
8	Layang–Layang	31	2305–2950	20–50	Non-serpentinised Peridotite	Eutric Leptic Cambisol (hypermagnesic)	< 0.3	Absent
9	Mesilau	25	1909–2067	< 20	Partially serpentinised Peridotite with Tremolite	Folic Hypereutric Cambisol (hypermagnesic)	< 1	Mor accumulation
10	Bukit Babi	18	1877–2286	20–50	Peridotite	Dystric Folic Cambisol (hypermagnesic)	< 1	Mor accumulation
11	Bambangan	27	1683–2077	50–75	Serpentinite	Mollic Leptosol (hypermagnesic)	< 1	Thin A–horizon
12	Bukit Hampuan	28	963–1336	50–75	Mixed	Mollic Leptosol (hypermagnesic)	0.5–1	Thin A–horizon
13	Nalumad	12	754–836	< 20	Peridotite	Plinthic Rhodic Ferralsol (magnesic)	> 5	Only leaf litter, iron concretions

TABLE 2

Ultramafic	Unit	Ultramafic bedrock (n = 76)		Non-ultramafic bedrock (n = 13)	
Al	%	0.02–19	3	0.1–10	5
Ca	%	0.01–12	2	0.002–10	1
Co	μg g^{-1}	3–27	8	3–11	5
Cr	μg g^{-1}	8–8604	1441	11–906	188
Cu	μg g^{-1}	0.1–620	46	0.1–170	25
Fe	%	0.06–43	5	0.1–5	2
K	%	0.01–3	0.3	0.01–2	1
Mg	%	0.05–53	19	0.1–28	5
Mn	μg g^{-1}	31–3264	1237	31–2869	560
Na	%	0.01–3	0	0.02–2	1
Ni	μg g^{-1}	16–4775	939	15–1315	225
P	μg g^{-1}	2.3–804	72	40–571	142
S	%	0.01–0.11	0.05	0.01–0.1	0.1
Si	%	0.4–36	15	2–36	21
Zn	μg g^{-1}	3.5–208	59	4–148	43

TABLE 3

Ultramafic	Extract	Unit	Ultramafic soils (n = 423)		Non-ultramafic soils (n = 67)	
Al	Total	mg g^{-1}	1.2–118	19	0.3–92	19
Ca	Total	μg g^{-1}	7.7–39,300	2433	2.2–12,380	541
Co	Total	μg g^{-1}	0.5–1524	253	0.5–26	7.7
Cr	Total	μg g^{-1}	121–21,710	3873	2.4–170	36
Cu	Total	μg g^{-1}	2.4–453	47	0.04–83	16
Fe	Total	mg g^{-1}	21–535	144	0.1–121	16
K	Total	μg g^{-1}	< 0.1–1056	93	38–7297	1065
Mg	Total	mg g^{-1}	0.3–235	32	0.03–18	1.9
Mn	Total	mg g^{-1}	0.04–34	3	< 0.01–1.5	0.1
Na	Total	μg g^{-1}	< 0.1–361	146	2.4–132	55
Ni	Total	μg g^{-1}	17–9308	1623	0.5–338	28
P	Total	μg g^{-1}	4.4–585	127	20–532	121
S	Total	μg g^{-1}	33–6172	371	64–641	212
Zn	Total	μg g^{-1}	13–373	107	1.2–111	19
pH	1:2.5 H_2O	–	3.8–9.7	6.0	3.5–7.2	4.6
EC	1:2.5 H_2O	μS	9.0–939	165	18–291	74
Al	DTPA	μg g^{-1}	0.03–522	14	2.5–850	337
Ca	Exch.	μg g^{-1}	0.6–6946	402	17–3394	125
Co	DTPA	μg g^{-1}	0.04–96	17	< 0.1–0.9	0.2
Cr	DTPA	μg g^{-1}	< 0.1–13	0.4	< 0.1–0.7	0.1
Cu	DTPA	μg g^{-1}	< 0.1–26	1.7	< 0.1–7.4	0.7
Fe	DTPA	μg g^{-1}	0.5–873	96	2.9–737	159
K	Exch.	μg g^{-1}	0.7–307	36	2.5–191	38
Mg	Exch.	μg g^{-1}	1.8–9155	942	0.2–57	12
Mn	DTPA	μg g^{-1}	0.4–822	215	0.1–40	3.6
Na	Exch.	μg g^{-1}	1.5–1652	103	0.2–89	11
Ni	DTPA	μg g^{-1}	0.2–442	62	0.03–3.3	0.3
P	ML-3	μg g^{-1}	< 0.1–32	2.7	1.7–80	12
S	DTPA	μg g^{-1}	0.9–683	24	1.0–33	6.5
Zn	DTPA	μg g^{-1}	0.02–161	1.2	0.05–16	0.9
Mg:Ca	Exch.	–	< 0.1–82	5.3	< 0.1–1.0	0.2

TABLE 4

Site	n	pH	Al*	Ca	Co	Cr*	Fe*	K	Mg*	Mn*	Ni
Bambangan	27	6.2	22.5	5990	214	3.7	95.8	75	40	2.8	1090
Bukit Babi	18	5.5	11.8	654	162	3.1	70.9	29	13	2.2	346
Bukit Hampuan	28	6.2	26.6	4028	318	4.7	137.8	90	28	3.9	1798
Layang-Layang	31	5.1	11.6	867	120	0.6	86.9	148	12	1.5	956
Marai Parai	34	5.3	21.3	698	69	3.4	75.8	44	24	0.7	442
Mesilau	25	6.2	12.4	909	156	0.7	78.6	136	57	2.0	1409
Serinsim	15	4.7	30.8	561	50	16.3	385.7	83	0.5	2.3	2452
Mt Tambuyukon summit	53	6.0	6.3	882	464	3.2	216.8	96	12.0	6.4	2137
Mt Tambuyukon slopes	12	5.5	17.9	651	737	8.8	312.0	83	4.9	7.7	2476
Wuluh River	35	7.3	5.5	1761	177	2.5	72.7	65	120	2.3	2268
Mt Nambuyukon	9	5.2	60.7	1186	165	3.8	188.2	87	6.2	2.1	779
Nalumad	12	4.6	31.4	578	124	6.1	233.2	160	0.6	3.1	902
Panataran Valley	26	6.5	26.5	9324	242	2.5	122.3	102	56	3.3	1496

TABLE 5

Site	n	Co	Fe	Mn	Ni	Al	Ca	K	Mg	Na	Mg:Ca	CEC	P
Bambangan	27	15	443	236	34	0.02	1.7	0.09	9.9	0.3	8.1	12.0	2.7
Bukit Babi	18	32	388	583	20	0.02	0.7	0.10	1.3	1.0	2.4	3.2	2.0
Bukit Hampuan	28	36	633	435	68	0.03	5.1	0.13	13.8	0.7	11.7	19.8	4.0
Layang-Layang	31	11	388	226	21	0.20	0.8	0.10	1.7	0.5	6.0	3.4	4.0
Marai Parai	34	4	98	73	13	0.12	0.3	0.05	1.0	0.1	3.8	1.6	1.8
Mesilau	25	9	616	157	31	0.02	1.3	0.08	10.1	0.2	12.8	11.8	3.5
Serinsim	15	2	73	30	3	0.04	0.3	0.08	0.2	0.1	0.8	0.6	1.3
Mt Tambuyukon summit	53	106	560	1512	139	0.01	1.1	0.09	3.5	1.1	5.7	5.8	1.1
Mt Tambuyukon slopes	12	156	528	1542	38	0.01	0.4	0.07	1.1	1.3	10.4	2.8	1.4
Wuluh River	35	20	553	259	152	0.09	1.2	0.06	14.6	0.1	21.4	16.0	2.3
Mt Nambuyukon	9	15	104	166	3	1.17	0.7	0.05	0.4	0.3	0.8	2.6	1.7
Nalumad	12	29	121	311	7	1.32	0.3	0.11	0.2	0.4	1.2	2.3	2.5
Panataran Valley	26	25	671	370	66	0.01	4.8	0.11	16.3	0.6	5.3	21.9	2.9

TABLE 6

Locality	Layang-Layang	Bambangan	Mt. Tambuyukon (summit)	Mt. Tambuyukon (summit)	Mesilau
Site number	8	11	1	1	9
Diopside	21.8	4.5	0.4	3.1	4.9
Tremolite	5	2.6	0.3	2.4	10.7
Antigorite	28.6	29.1	32.1	24.3	23.8
Lizardite	7.5	17.8	26.8	27.2	12.9
Spinel	2.9	8.1	5.7	7.3	9.2
Talc	4.2	4.9	1.5	2.7	5.5
Forsterite	29.7	32.6	33	32.6	32.6
Smectite group clays	0.3	0.4	0.3	0.3	0.4
Al %	1.7	1.1	0.03	0.02	0.4
Ca %	4.4	0.2	0.02	0.2	0.7
Co	6	8	9	8	10
Cr	1287	2735	239	212	1571
Cu	19	36	13	33	5
Fe %	6.1	5.6	2.5	4.5	5
K %	0.02	0.007	0.009	0.003	0.005
Mg %	20.4	29.4	16.5	24.7	22.2
Mn	1394	1287	867	1089	1486
Na %	0.08	0.01	0.03	0.01	0.01
Ni	775	1205	1265	1266	1078
P	52	25	13	23	27
S %	0.04	0.09	0.06	0.02	0.04
Si %	14.5	16.1	13.4	12.5	9.3
Ti	963	124	31	22	85
Zn	45	75	44	59	69

TABLE 7

Locality	Bambangan	Bukit Babi	Layang-Layang	Marai Parai	Mesilau	Mt Tambuyukon	Mt Tambuyukon	Wuluh River	Serinsim
Site number	11	10	8	7	9	1	1	3	4
Diopside	0.5	1.4	3.5	1.1	2.8	1.3	2.4	0	1.5
Tremolite	12.7	22.4	22.8	17.2	25.9	13.7	16.5	0	17.3
Antigorite	21	28.1	24.5	25.9	23.1	22.4	19.2	23.1	18
Lizardite	9	9.7	8.7	8.4	7.5	11	7.6	35.1	6.7
Spinel	8	5.8	10.4	6	7.4	14.1	13.6	10.9	28.9
Talc	27.2	11.5	1.9	15.3	11.1	7.5	17.1	1.8	5
Forsterite	20.6	19.7	17.8	24.9	20	28.6	22.5	28.7	21.4
Smectite group clays	1	1.5	1.4	1.2	2.2	1.3	1.1	0.4	1.1
Al*	28.7	26.8	39.7	18.9	29.5	5.4	6.5	2.1	33.5
Ca	3990	670	2524	446	2788	510	325	75	28
Co	236	102	63	72	176	417	185	103	4
Cr	4071	2800	474	4934	1176	1742	1494	899	10,530
Cu	21	13	56	21	28	15	7	3	50
Fe*	101.6	88.4	73	216.1	155.4	238.2	164.5	43	349
K	19	56	1904	23	68	32	39	< 0.01	< 0.01
Mg*	30.2	42.1	11.8	15	35.3	13.4	6.4	198.7	1.5
Mn	4115	1441	748	1193	2534	7582	3120	922	2508
Na	61	16	113	< 0.01	115	53	37	< 0.01	< 0.01
Ni	641	487	236	773	1368	2031	1109	1131	2609
P	77	62	167	81	130	116	42	11	205
S	318	343	531	395	296	415	367	89	1881

TABLE 8

Depth (m)	pH	EC	Ca	K	Mg	Mg:Ca	Al*	Co	Cr*	Fe*	Mn	Ni	Ni ML-3	P	Si
Sunsui															
0–5	4.4	55	224	13	17	0.1	16	5	0.9	76	96	55	1.1	43	–
5–9	5.7	12	226	13	237	1.1	19	18	1.0	98	408	144	3.5	35	–
5–9	5.8	169	611	51	2142	3.5	27	150	1.1	109	3157	1478	92	142	–
9–10	6.1	891	667	34	3996	6.0	17	66	0.8	51	467	1960	318	51	–
10–14	6.3	196	744	129	4852	6.5	17	114	0.9	102	2014	1810	52	100	–
14–18	6.7	100	905	57	6179	6.8	18	180	0.8	91	2043	2083	43	104	–
18–22	6.9	195	1043	90	3423	3.3	6	157	0.8	86	1648	3072	111	32	–
Bedrock	–	–	6	1	420	–	9	70	694	68	1210	953	–	49	226
Hampuan															
0–4	6.0	18	231	13	18	0.1	100	878	14.6	395	6931	2509	0.4	106	–
4–7	6.2	10	230	13	137	0.6	92	671	15.8	383	7033	3583	2.1	92	–
7–16	5.6	13	220	16	31	0.1	89	1055	15.8	372	8106	3101	0.7	74	–
16–26	6.5	55	465	9.2	3389	7.3	37	1040	14.0	352	8728	6985	44	47	–
26–30	7.6	85	686	11	6312	9.2	13	694	5.1	254	7540	9308	102	41	–
30–36	7.2	132	950	5.2	9155	9.6	34	597	9.0	176	7512	7164	129	20	–
Bedrock	–	–	12	0.2	126	–	7	8	1244	23	1032	963	–	67	3.9
Serinsim															
0–0.1	5.1	74	207	29	28	0.1	33	151	17.6	426	4754	2532	19	443	–
0.3–0.4	5.3	55	208	14	12	0.1	31	19	16.9	407	3243	2622	1.9	149	–
0.8–0.9	5.3	29	212	6.6	10	0.0	36	181	19.9	453	3493	3205	0.7	186	–
Bedrock	–	–	0.4	0.4	256	–	6	13	1909	57	3124	2460	–	53	11
Wuluh River 1															
0–0.05	6.4	180	236	36	1733	7.3	2.5	93	2.2	41	1358	1835	68	80	–
0.5–0.1	7.1	116	220	23	1115	5.1	2.6	96	2.4	40	1292	1669	52	59	–
0.1–0.3	7.4	112	197	4.5	331	1.7	2.3	107	2.4	45	1517	2181	18	12	–
0.3–0.5	8.5	142	180	1.8	173	1.0	2.3	86	2.7	40	1310	1723	2.1	20	–
0.5–0.75	9.2	726	204	5.1	6218	30.4	2.1	82	2.1	39	1233	1829	6.6	13	–
Bedrock	–	–	1.8	0.05	326	–	4.7	8	2455	42.5	860	1111	–	24	13

TABLE 9

Soil parameter	Unit	Cuba	Brazil*	New Caledonia	Indonesia (Sulawesi)	Indonesia (Sulawesi)	Indonesia (Mt Piapi)	Philippines Mt Giting-Giting	Malaysia (Mt Kinabalu)
Altitude	m asl	–	750–1100	–	–	200–300	60–500	325–1540	400–2900
pH	–	–		4.4–6.9	5.3–6.3	5.8–6.1	6.1–6.4	4.3–5.5	3.8–9.7
CEC	cmol$^{(+)}$ kg^{-1}	–	0.3–82.9	1.2–34		43–67[f]	15–44	–	0.03–128[a]
Mg:Ca	–	–	8.3–24	0.8–23	0.9–5.7	0.6–2.1[f]	1.6–32	0.3–2.9[b]	0.1–136[a]
Ca (exch.)	cmol$^{(+)}$ kg^{-1}	–	0.015–1.9	0.01–1.8	4.6–13.3	0.6–0.1[f]	0.9–16	0.5–3.4[b]	0.003–35[a]
Ca (pseudo-total)	µg g^{-1}	4800	0–13,500	–	–	–	–	–	7.7–39,300
Mg (exch.)	cmol$^{(+)}$ kg^{-1}	–	0.004–1.9	0.2–38.5	11.1–26.2	0.52–1.18[f]	13.9–27.3	0.75–3.64[b]	0.02–76[a]
Mg (pseudo-total)	mg g^{-1}	–	12–154	–	–	–		–	0.27–235
K (exch.)	cmol$^{(+)}$ kg^{-1}	–	–	0.02–0.2	0.05–0.5	0.03–0.10[f]	0.19–0.38	0.04–0.41[b]	0.002–0.79[a]
K (pseudo-total)	µg g^{-1}	740	–	–	–	5164–6260[d]	–	–	0.1–1056
P (pseudo-total)	µg g^{-1}	1724	< 100	393–509	–	95–237[d]	–	–	4.4–585
P (extract.)	µg g^{-1}		–	140–310	–	1.7–3.8[g]	0.94–6.8[c]	0.41–2.07[c]	0.1–32[i]
Fe (pseudo-total)	mg g^{-1}	196	154–466	–	–	132–293	–	–	21–535
Ni (pseudo-total)	µg g^{-1}	4674	7744–18,520	1300–10,400	825–4050	3730–7051[d]	–	–	17–9308
Ni (extract.)	µg g^{-1}		0–1232	0.2–66		6.0–7.5[f]	8.5–37[e]	1–24[e]	0.17–442[h]
Cr (pseudo-total)	mg g^{-1}	3.8	11,200–46,800	6.3–56	1.0–9.9	9.5–17[d]	–	–	121–21,710
Cr (extract.)	µg g^{-1}	–	80–980	0.6–8.1	1	–	–	–	< 0.1–13[h]
Co (pseudo-total)	µg g^{-1}	381	413–799	230–1300	–	57–337[d]	–	–	0.5–1524
Co (extract.)	µg g^{-1}	–	–	76–116[h]	–		–	–	0.04–96[h]
References		Reeves et al., 1999	Raous et al., 2013	Jaffré, 1980	Parry, 1985	Tjoa, unpublished; van der Ent et al., 2013	Proctor et al., 1994	Proctor et al., 1998	This research